

Plant genotype influences aquatic-terrestrial ecosystem linkages through timing and composition of insect emergence

ZACCHAEUS G. COMPSON,^{1,2,3,5,†} BRUCE A. HUNGATE,^{1,2,3} THOMAS G. WHITHAM,^{2,3} NASHIELLY MENESES,^{2,3} POSY E. BUSBY,⁴ TODD WOJTOWICZ,^{2,3} AUDREY C. FORD,^{2,3,6} KENNETH J. ADAMS,^{2,3,7} AND JANE C. MARKS^{1,2,3}

¹Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona 86011-5620 USA

²Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, Arizona 86011-6077 USA

³Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011-6077 USA

⁴Department of Biology, Duke University, Durham, North Carolina 27708 USA

Citation: Compson, Z. G., B. A. Hungate, T. G. Whitham, N. Meneses, P. E. Busby, T. Wojtowicz, A. C. Ford, K. J. Adams, and J. C. Marks. 2016. Plant genotype influences aquatic-terrestrial ecosystem linkages through timing and composition of insect emergence. *Ecosphere* 7(5):e01331. 10.1002/ecs2.1331

Abstract. Terrestrial leaf litter provides aquatic insects with an energy source and habitat structure, and species differences in litter can influence aquatic insect emergence. Emerging insects also provide energy to riparian predators. We hypothesized that plant genetics would influence the composition and timing of emerging insect communities among individual genotypes of *Populus angustifolia* varying in litter traits. We also compared the composition and timing of emerging insect communities on litter from mixed genotypes of three cross types of a hybridizing cottonwood complex: *P. angustifolia*, *P. fremontii*, and their F₁ hybrids. Using litter harvested from an experimental common garden, we measured emerging insect community composition, abundance, and production for 12 weeks in large litter packs affixed with emergence traps. Five major findings emerged. (1) In support of the genetic similarity hypothesis, we found that, among *P. angustifolia* tree genotypes, litter from more closely related genotypes had more similar litter thickness, nitrogen concentrations, decomposition rates, and emerging insect communities. (2) Genetic similarity was not correlated with other litter traits, although the litter fungal community was a strong predictor of emerging insect communities. (3) Litter decomposition rate, which was the strongest predictor of emerging aquatic insect communities, was influenced by litter thickness, litter N, and the litter fungal community. (4) In contrast to strong community composition differences among *P. angustifolia* genotypes, differences in community composition between *P. fremontii* and *P. angustifolia* were only marginally significant, and communities on F₁ hybrids were indistinguishable from *P. angustifolia* despite genetic and litter trait differences. (5) Mixed litter packs muted the genetic effects observed in litter packs consisting of single genotypes. These results demonstrate that the genetic structure of riparian forests can affect the composition and timing of aquatic insect emergence. Because many riparian trees are clonal, including *P. angustifolia*, large clone size is likely to result in patches of genetically structured leaf litter that may influence the timing and composition of insect emergence within watersheds. Riparian restoration efforts incorporating different tree genotypes could also influence the biodiversity of emerging aquatic insects. Our work illustrates the importance of plant genes for community and ecosystem processes in riparian corridors.

Key words: aquatic insect communities; common garden; genetic similarity hypothesis; genotypes; headwater stream; hybrids; insect emergence; leaf litter; Oak Creek, Arizona; *Populus angustifolia*; *Populus fremontii*; secondary production.

Received 28 July 2015; revised 10 November 2015; accepted 7 December 2015. Corresponding Editor: J. Benstead.

Copyright: © 2016 Compson et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

⁵ Present Address: Canadian Rivers Institute, University of New Brunswick, Fredericton, New Brunswick E3B 5A3 Canada.

⁶ Present address: Mechanical Engineering Department, University of California, Berkeley, California 94720-1740 USA.

⁷ Present address: George Washington Memorial Parkway, US National Park Service, McLean, Virginia 22101 USA.

† E-mail: zacchaeus.greg.compson@gmail.com

INTRODUCTION

Aquatic insects are an important food for riparian predators, including birds (Gray 1993, McIntosh 2000), bats (Barclay 1991, de Jong and Ahlén 1991, Sullivan et al. 1993), lizards (Sabo and Power 2002), and spiders (Sanzone et al. 2003, Paetold et al. 2005). The insect species emerging from the water depend on properties within the river and the surrounding landscape. For example, the bottom-up effects of nutrient enrichment can increase emerging insect production (Greig et al. 2012), whereas the top down effects of fish predation can decrease emerging insect abundance and production and alter community composition (Baxter et al. 2004, Wesner 2010, Benjamin et al. 2011, Greig et al. 2012). At the landscape scale, forested catchments tend to have higher emerging insect abundance of indicator taxa (i.e., Ephemeroptera, Plecoptera, Trichoptera) and different community composition compared to unforested catchments (Collier et al. 1997, Winterbourn et al. 2007). Management within the catchment also affects emerging insects, with forested catchments tending to have higher total abundance and diversity of emerging insects than deforested or grazed watersheds (Briers et al. 2002, Harrison and Harris 2002, Briers and Gee 2004). Because leaf litter constitutes a substantial flow of energy into the aquatic ecosystem (Fisher and Likens 1973, Meyer et al. 1998), these inputs are particularly important to aquatic invertebrates, especially in headwater streams (Webster et al. 1995, Webster and Meyer 1997).

The species composition of a riparian forest may strongly influence aquatic invertebrates and associated ecosystem functions. In streams, leaf litter of different plant species decomposes at different rates, affecting the abundance and community composition of associated invertebrates and microbes (Graça 2001, Tank et al. 2010). In addition, litter from different plant species influences growth and survival of shredding insects and tadpoles (Canhoto and Graça 1992, 1995, Cohen et al. 2012, Stoler and Relyea 2013). Variation in litter traits also influences the abundance and diversity of emerging aquatic insects (Kominoski et al. 2012, Compson et al. 2013). Yet, little is known about how intraspecific variation in litter influences ecosystem function and aquatic invertebrates, including aquatic emergence.

Genetic variation within tree species influences associated communities, including understory and epiphytic plants (Crutsinger et al. 2008, 2010, Zytynska et al. 2011), epiphytic lichens (Lamit et al. 2011), fungal pathogens (Busby et al. 2013), soil microbes (Schweitzer et al. 2008), and foliar arthropods (Fritz and Price 1988, Dungey et al. 2000, Van Zandt and Agrawal 2004). The genetic similarity hypothesis predicts that plants with more similar genotypes will support more similar traits (e.g., phytochemistry), which in turn are associated with more similar arthropod communities (sensu Bangert et al. 2006b). The afterlife effects (sensu Findlay et al. 1996) of plant genes on litter communities are much less understood, though specific litter taxa have been shown to respond to intraspecific plant variation (Barbour et al. 2009a, Wojtowicz et al. 2014). Variation within tree species can also influence litter decomposition and invertebrate communities in terrestrial (Schweitzer et al. 2005, Whitham et al. 2012) and aquatic (LeRoy et al. 2006, 2007, Lecerf and Chauvet 2008, Jackrel and Wootton 2014) ecosystems.

Here, we examined how intraspecific and interspecific genetic variation within a cottonwood hybridizing system (*Populus angustifolia* × *P. fremontii*) influences the composition and timing of emerging insects. We compared emerging insect community composition, abundance, and production among leaf litter of *P. angustifolia* genetic isolates and also of mixed genotypes for the two parent species and their F₁ hybrids. We tested five hypotheses. (1) Within *P. angustifolia*, genetic similarity of plants correlates with community similarity of emerging insects. (2) Emerging aquatic insect abundance, production, and diversity are higher from packs with mixed cross type litter relative to single *P. angustifolia* genotypes. (3) Functional feeding groups, indicator taxa, and other taxonomic groups that feed on leaf litter respond to cross type and genotype litter differences. (4) Emerging insect communities, abundance, and production vary temporally in relation to litter decomposition rates. (5) Variation in litter chemical and physical traits is associated with variation in emerging insect communities, abundance, and production.

The rationale for our first hypothesis was the positive association between genetic similarity and arthropod community similarity that has been documented in temperate cottonwood

forests (Bangert et al. 2006a, b, Ferrier et al. 2012), eucalypt forests (Barbour et al. 2009b), and rain forests (Zytnska et al. 2011, 2012). Our second hypothesis was postulated because plant genotypic diversity increases associated arthropod diversity (Crutsinger et al. 2006, Johnson et al. 2006, Ferrier et al. 2012) in terrestrial ecosystems. In addition, leaf litter mixtures are expected to provide a more continuous food source for aquatic insects (*sensu* Hynes 1975) because the presence of slow-decomposing litter may disproportionately extend the length of time fast-decomposing litter is available to aquatic insects (Palmer et al. 2000, Swan and Palmer 2004). The rationale for our third hypothesis was based on the observation that shredders can discriminate among leaf litter in the lab (Canhoto and Graça 1992, 1995, Nolen and Pearson 1993, Schulze and Walker 1997) and the field (Webster and Benfield 1986, Basaguren and Pozo 1994, Malmqvist and Oberle 1995). In addition, Ephemeroptera, Plecoptera, and Trichoptera have been shown to vary in emergence rates between *Populus* litter species (Compson et al. 2013) and can be important indicators of water quality (Lenat 1988, Plafkin et al. 1989, Bain et al. 2000), which could vary among litter packs if the litter differentially leaches organic compounds. Our fourth hypothesis was based on the idea that aquatic insect emergence should be enhanced in areas that retain and provide predation refuge for benthic insects (Power and Rainey 2000, Power et al. 2004); this, coupled with known litter decomposition rate differences (LeRoy et al. 2006, 2007) and structural variation among *Populus* cross types and genotypes (Table 1, 2), led to the prediction that cross types and genotypes of litter with fast decomposition rates would have higher initial emergence rates, whereas those with slow decomposition rates would retain material and structure longer, leading to higher emergence rates toward the end of the experiment. Our final hypothesis was based on the findings that, in hybridizing cottonwoods, trees grown in common gardens predictably vary in plant traits that correlate with litter decomposition and associated arthropod and microbial communities (Whitham et al. 2006 and references therein, Wymore et al. 2013). Specifically, we predicted that emerging insect abundance and production would be higher from slow-decomposing compared to fast-decomposing

cross type and genotype litter because slow-decomposing *Populus angustifolia* litter has higher emergence rates (Compson et al. 2013) and fluxes of C and N to insects (Compson et al. 2015) compared to fast-decomposing *Populus fremontii* litter. The high amount of phenotypic variation in the *Populus* complex (Holeski et al. 2012 and references therein), particularly among *P. angustifolia* genotypes, provides a template for studying how a suite of litter quality traits (Table 1, 2) affects emergence.

METHODS

Study design

Leaf litter from seven *P. angustifolia* genotypes ($n = 4\text{--}11$ replicates per genotype) was selected based on known phytochemical differences (B. Rehill, personal communication) to determine whether intraspecific variation in litter influences abundance ($\text{no. m}^{-2}\cdot\text{d}^{-1}$), production ($\text{mg dry weight}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), diversity (Shannon's H'), and community composition of emerging aquatic insects. Litter (250 g) from individual clones of each genotype was used in replicate litter packs. In addition, litter from three cross types (*P. fremontii*, *P. angustifolia*, and *P. fremontii* \times *P. angustifolia* F_1 hybrids) was included. Cross type litter (250 g per replicate) represented mixtures of 8–12 genotypes each of *P. fremontii*, F_1 hybrid, or *P. angustifolia* genotypes ($n = 14$ replicate mixtures per cross type). Litter was collected from a 20-yr-old cottonwood common garden in Ogden, UT, during the fall of 2008. Trees were the same age and growing under similar environmental conditions, making it possible to limit the effect of environment and isolate the genetic influences on plant litter traits. Whole-tree nets constructed of bridal veil enclosed all branches. The tops of the nets were closed to prevent litter from blowing in from other trees in the garden. Litter nets were erected in early October, when leaves were just starting to change color, and collected at the end of November, after litter abscission. No major precipitation events occurred during litter netting.

The experiment was conducted over 86 d in upper Oak Creek, AZ, upstream of Cave Spring Campground, from November, 2009, through January, 2010 (Fig. 1). Oak Creek has an intact

Table 1. Summary of mean leaf litter traits (\pm SE) for *Populus angustifolia* genotypes. Percentages are expressed on a dry mass basis, $\text{g g}^{-1} \times 100\%$.

	996	1008	1012	1017	1020	RM2	T15
Chemistry							
Lignin (%)	26 \pm 1.3	20 \pm 1.8	25 \pm 0.90	26 \pm 1.7	28 \pm 3.4	28 \pm 2.1	21 \pm 2.5
Tannin (%)	2.6 \pm 0.29	0.72 \pm 0.13	1.7 \pm 0.20	2.5 \pm 0.74	1.3 \pm 0.52	1.2 \pm 0.38	0.39 \pm 0.24
N (%)	1.0 \pm 0.051	1.2 \pm 0.11	1.6 \pm 0.057	0.86 \pm 0.055	1.6 \pm 0.20	1.30 \pm 0.095	1.60 \pm 0.19
C:N (gC gN ⁻¹)	42 \pm 2.1	34 \pm 3.1	27 \pm 0.97	50 \pm 3.2	27 \pm 3.2	34 \pm 2.6	28 \pm 3.4
Structure							
Density (g cm ⁻³)	0.019 \pm 0.0015	0.016 \pm 0.00080	0.016 \pm 0.0025	0.012 \pm 0.0012	0.017 \pm 0.0014	0.015 \pm 0.0032	0.012 \pm 0.0011
Thickness (mm)	0.17 \pm 0.011	0.15 \pm 0.013	0.15 \pm 0.0048	0.16 \pm 0.010	0.16 \pm 0.010	0.15 \pm 0.013	0.13 \pm 0.014
Decomposition (k d ⁻¹)	0.019 \pm 0.0021	0.021 \pm 0.0032	0.022 \pm 0.0017	0.021 \pm 0.0025	0.017 \pm 0.0024	0.028 \pm 0.0036	0.025 \pm 0.0028
Pathogen damage (% leaf area), 2009							
<i>D. populi</i>	0.72 \pm 0.28	1.9 \pm 0.72	0.58 \pm 0.46	0.19 \pm 0.11	1.6 \pm 0.59	1.2 \pm 0.79	0.21 \pm 0.13
Mycosphaerella	4.0 \pm 0.86	4.5 \pm 0.67	2.2 \pm 0.32	2.2 \pm 0.26	3.5 \pm 0.62	4.1 \pm 1.9	12 \pm 3.8
<i>P. populi</i>	0.92 \pm 0.077	0.63 \pm 0.18	0.52 \pm 0.16	0.71 \pm 0.13	0.45 \pm 0.15	0.40 \pm 0.24	0.85 \pm 0.15
Pathogen damage (% leaf area), 2010							
<i>D. populi</i>	2.1 \pm 0.54	9.2 \pm 1.9	1.8 \pm 0.76	2.2 \pm 0.55	7.0 \pm 0.65	2.5 \pm 0.45	0.67 \pm 0.42
Mycosphaerella	4.1 \pm 0.61	1.6 \pm 0.38	2.5 \pm 0.65	1.1 \pm 0.21	2.6 \pm 0.89	4.3 \pm 2.1	8.9 \pm 3.0
<i>P. populi</i>	0.89 \pm 0.058	0.87 \pm 0.082	0.81 \pm 0.013	0.83 \pm 0.096	1.0 \pm 0.00	0.92 \pm 0.083	1.1 \pm 0.19

cottonwood hybrid zone with *P. fremontii* and *P. angustifolia* trees. Within this hybrid zone, we randomly distributed large litter packs along a ~100-m riffle-run reach at equal depth (~16 cm) and at least 1 m apart to avoid flow interference (Fig. 1). These litter packs were large enough (0.5 \times 0.5 \times 0.16 m) to measure insect emergence from large litter aggregates commonly found at Oak Creek in the autumn (Z. Compson, *personal*

observation). Litter packs were covered with Vexar (mesh size 10 \times 4 mm), allowing immigration and emigration of aquatic insects while excluding the effects of fish. Microfiber emergence nets were attached to the top of litter packs, just above water level, and acrylic collectors filled with ~100 mL 70% ethanol were set weekly for 48 h starting on day 7 ($n = 12$ weeks). During the final harvest, litter and associated insects were

Table 2. Summary of mean leaf litter traits (\pm SE) for *Populus* cross types. Percentages are expressed on a dry mass basis, $\text{g g}^{-1} \times 100\%$.

	<i>P. fremontii</i>	F1 hybrid	<i>P. angustifolia</i>
Chemistry			
Lignin (%)	11 \pm 0.60	23 \pm 1.8	27 \pm 0.80
Tannin (%)	0.27 \pm 0.020	4.2 \pm 0.35	3.0 \pm 0.16
N (%)	0.71 \pm 0.090	0.72 \pm 0.028	1.2 \pm 0.071
C:N (g C/g N)	59 \pm 7.0	59 \pm 2.7	40 \pm 2.3
Structure			
Density (g cm ⁻³)	0.0074 \pm 0.00023	0.0089 \pm 0.00038	0.020 \pm 0.00039
Thickness (mm)	0.17 \pm 0.0023	0.21 \pm 0.0054	0.16 \pm 0.0056
Decomposition (k d ⁻¹)	0.028 \pm 0.0013	0.030 \pm 0.0022	0.026 \pm 0.0024
Pathogen Damage (% leaf area), 2009			
<i>D. populi</i>	0.0	0.25 \pm 0.11	2.1 \pm 0.50
Mycosphaerella	1.1 \pm 0.42	2.8 \pm 0.35	4.6 \pm 0.47
<i>P. populi</i>	0.13 \pm 0.13	0.54 \pm 0.10	0.65 \pm 0.042
Pathogen Damage (% leaf area), 2010			
<i>D. populi</i>	1.6 \pm 0.64	2.2 \pm 0.44	6.5 \pm 1.2
Mycosphaerella	0.40 \pm 0.14	0.58 \pm 0.19	3.6 \pm 0.37
<i>P. populi</i>	0.18 \pm 0.14	0.70 \pm 0.12	0.86 \pm 0.047

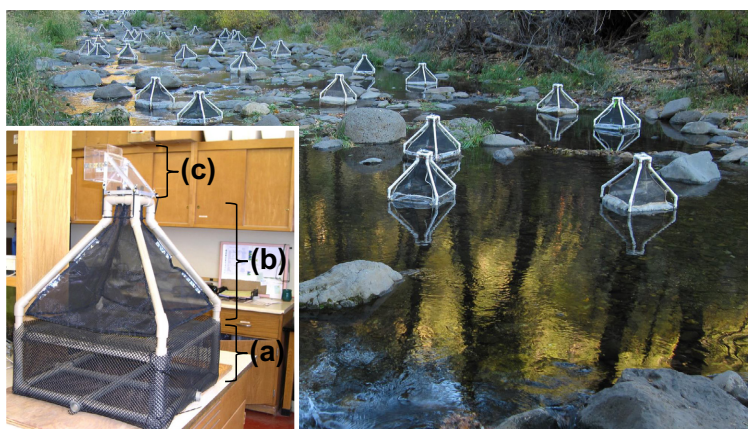


Fig. 1. Photograph of the downstream section of the study reach in upper Oak Creek, AZ, near Cave Springs Campground. (a) Large litter packs were affixed with (b) pyramidal emergence nets and emerging insects were collected once a week using (c) transparent acrylic collectors filled with 70% ethanol that were set above nets for 48 h (inset). Photographs by Z. Compson.

collected from each pack. Midway through the experiment (21 December, 2009), basic water chemistry parameters were measured during base-flow conditions. Measurements were taken approximately 0.25 meters downstream of each litter pack using a Hach Hydrolab (values depict means \pm standard errors): temperature ($10 \pm 0.03^\circ\text{C}$), pH (8.5 ± 0.74), specific conductivity ($290 \pm 0.08 \mu\text{S/cm}$), salinity ($0.14 \pm 0.00 \text{ p.p.t.}$), total dissolved solids ($0.19 \pm 0.00 \text{ g/L}$), and dissolved oxygen ($98 \pm 0.06\%$ saturation). In addition, stream flow was marginally lower downstream ($17.4 \pm 1.17 \text{ m/s}$) compared to upstream ($19.7 \pm 1.16 \text{ m/s}$) of packs (paired t -test: $t_{94} = -1.6$; $P = 0.056$), but was not affected by litter type, either for genotype ($F_{6,41} = 0.10$; $P = 0.99$) or cross type litter ($F_{3,41} = 1.1$; $P = 0.35$).

Emerging insects

Clear acrylic traps were attached above the emergence nets (Fig. 1, inset) and, after 48 h, traps were removed and the 70% ethanol and captured insects were collected in 250-mL cups. Insects were sorted at $2\times$ magnification and identified down to the lowest taxonomic level possible using Leica MZ75 dissecting microscopes at $6.3\times$ to $50\times$ magnification. Insects were identified using aquatic insect keys (e.g., Merritt and Cummins 1996) and reference collections were established at NAU's Colorado Plateau Biodiversity Center. Insects were identified to

species (6.3% of taxa), genus (17% of taxa), or family (77% of taxa). Insects that could not be identified past family were morphotyped when there were clear morphological differences within a family (38% of taxa). Insect counts and body lengths were recorded. In total, we censused 191 788 insects of 64 taxa across eight orders. Biomass was calculated using length-mass algorithms developed for emerging aquatic insects (Sample et al. 1993, Sabo et al. 2002).

Cage effects of large litter packs

Because emerging insect abundance and production may have been enhanced due to altered abiotic variables and predator release caused by cages (Woodin 1974, Hulberg and Oliver 1980, Peckarsky 1985, Power et al. 2004), we included empty packs (no litter) to determine emerging insect abundance and production attributed to the litter packs themselves. Averaged across the entire 12-week study, control cages yielded 271 ± 30.6 insects ($\text{no. m}^{-2}\cdot\text{d}^{-1}$) and $100 \pm 11.1 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. These production rates were 1.7-times (Jackson and Fisher 1986) and 2.9-times (Grimm 1987) higher than ambient emergence documented from a nearby desert stream (Sycamore Creek, AZ). Packs with litter yielded 12% to 37% higher emerging insect abundance and 13% to 40% higher production compared to packs with no litter. While the emergence rates measured in our study were

likely higher than ambient rates, the rates we measured are potentially more realistic in the context of headwater streams, which are known to have relatively high retention rates (Wallace et al. 1995, Webster et al. 1999, Hoover et al. 2006) and accumulate discrete litter patches of abundant resources for detritivores following autumn litter drop (Casas 1997, Rowe and Richardson 2001, Kobayashi and Kagaya 2002); this is the case in Oak Creek, where natural litter packs can be substantial (Z. Compson, personal observation) and *Populus* litter retention rates in riffles (mean $k \pm$ standard error = $0.061 \pm 0.0099 \text{ m}^{-1}$, Z. Compson, unpublished data) are much higher compared to retention rates reported in a nearby system (Compson et al. 2009). Regardless of the effect of cages on emergence rates, our main focus was on estimating the effects of litter type on emergence, and these estimates were likely conservative because small-scale cage experiments on benthic invertebrates may underestimate treatment effects (Kohler and Wiley 1997). Inferences made in our study involved comparing litter packs containing different litter types with the same cage effects. We restrict our interpretation to the ecological significance of the treatment effects, rather than the magnitudes of measured emergence rates.

Leaf litter traits proposed to influence aquatic insect emergence

We measured genetic distance and chemical and physical litter traits among genotypes to test their effect on the community composition, abundance ($\text{no. m}^{-2} \cdot \text{d}^{-1}$), and production ($\text{mg dry weight m}^{-2} \cdot \text{d}^{-1}$) of emerging insects.

Genetic distance.—Using GenAlEx (Peakall and Smouse 2006, 2012), we calculated the pairwise genetic distance among *P. angustifolia* individuals. Cottonwood samples were fingerprinted at fourteen MSAT loci (GCPM_772, ORPM 60, GCPM_2903, PMGC_333, GCPM_2315, GCPM_2425, GCPM_2992, GCPM3592, GCPM_3907, GCPM_961, GCPM_2900, GCPM_3681, GCPM_1685, GCPM3457; Tuskan et al. 2004; http://www.ornl.gov/sci/ipgc/ssr_resource.htm). These loci targeted specific sections of linkage regions, and most of the loci amplified different linkage regions. All samples were amplified at the same 14 loci. Fragment analysis was performed using GeneMapper (Applied Biosystems 2006). Repeatability of allele assignments was assessed

in at least two independent PCR amplifications with the samples rearranged on plates.

Litter chemistry.—A subsample of initial litter from each litter pack was set aside for chemical analysis of % lignin, % condensed tannins, %C, and %N. Chemical analysis of lignin and condensed tannins was conducted at the Lindroth Chemical Ecology Lab at the University of Wisconsin, Madison. Dried litter was ground with a Wiley mill (mesh size #40), freeze-dried, and stored at -20°C . Litter lignin concentrations were assessed by digesting ground plant material ($\sim 500 \text{ mg}$) in hot cetyltrimethylammonium bromide acidified with H_2SO_4 to determine fiber concentrations and then performing a subsequent digestion in 72% H_2SO_4 . Condensed tannins, important secondary metabolites in *Populus* (Palo 1984, Lindroth et al. 1987, Rehill et al. 2005, 2006), were assessed using the acid butanol assay (Porter et al. 1986) with purified *P. angustifolia* condensed tannins as standards (Rehill et al. 2006). Litter %C and %N were measured at the Colorado Plateau Stable Isotope Laboratory (CPSIL, <http://www.isotope.nau.edu>) using a Thermo Finnigan Flash 1112 elemental analyzer (Thermo Finnigan, San Jose, California, USA).

Litter structure.—Structure was measured using two metrics. First, litter bulk density (g cm^{-3}) was measured as the mass of bulk litter without compaction that would fit in a 1.5 L container. Second, litter thickness (mm) was measured using digital calipers at five points on each piece of litter: the center, to the right of the mid-vein, on the (1) bottom, (2) middle, and (3) top of each piece, and the middle of the (4) first and (5) final third of each piece along the widest horizontal axis. Mean litter thickness was calculated for each piece of litter, and a mean of 10 pieces were used for each replicate.

Litter fungal community.—The fungal pathogen species (*Drepanopeziza populi* (Helotiales), *Phyllactinia populi* (Erysiphales), and *Mycosphaerella* spp. (Capnodiales) that caused visible symptoms of disease on living leaves were assessed in September of 2009 and 2010 in the Ogden Nature Center common garden (Busby et al. 2013). For each leaf ($n = 24$ per tree), a visual estimate of leaf pathogen severity was assessed on a scale from 0 to 5 (0 = no damage, 1 = 1–6%, 2 = 7–12%, 3 = 13–25%, 4 = 26–50% or 5 = >50%), and from these scores a single, weighted damage score was calculated

(Dirzo and Domínguez 1995). Fungal pathogens were not measured on the leaf litter used in our study (from 2008) because not enough litter remained from that year for some genotypes. Fungal pathogen community composition and individual species abundances represent heritable traits (Busby et al. 2013) and are consistent from year to year (2009 compared to 2010: R^2 : *D. populi* = 0.52; *Mycosphaerella* spp. = 0.38; *P. populi* = 0.43).

Decomposition.—Remaining leaf litter and benthic aquatic insects from litter packs were harvested after the final collection of emerging insects (day 77) and placed on ice. Litter packs were processed within 48 h of harvesting. Benthic sediment and invertebrates were separated using 250 μm sieves and invertebrates were preserved in 70% ethanol. Remaining litter was rinsed with deionized water and dried at 70°C for 96 h. Dried litter was weighed on a Mettler Toledo microbalance, ground in a Wiley Mill to 425 μm , and combusted at 550°C in a muffle furnace (Barnstead International, Dubuque, Iowa, USA) for 1 h to determine ash-free dry mass (AFDM) according to the methods of Benfield (2006).

Data analysis.—We conducted Mantel and partial-Mantel tests in R (R Core Team 2015) using the ecodist package (Goslee and Urban 2007) to test if the genetic distance matrix correlated with the community dissimilarity matrix. Mantel tests were used to examine associations among tree genetic distance, aquatic insect community dissimilarity, and leaf litter traits, including lignin (%), condensed tannins (%), litter density (g/cm^3), litter thickness (mm), litter N (%), litter C:N, the litter fungal community, and decomposition (k/d). Partial-Mantel tests were used to construct path diagrams because they show associations between variables with all other variables held constant. Two path models were constructed. The first model assessed litter traits independently as mechanisms for how genetic distance influences emerging insect communities. Because litter traits, particularly litter chemistry, are known to influence decomposition (Cornwell et al. 2008), the second model assessed how litter traits influence litter decomposition and how litter decomposition then influences emerging insect communities. As recommended by McCune et al. (2002), com-

munity data were relativized by taxa total abundance and a Bray–Curtis dissimilarity matrix was calculated; litter trait data were relativized by Euclidean distances and Euclidean dissimilarity matrices were calculated. For all Mantel and partial-Mantel tests, dissimilarity matrices were compared and p-values were calculated using distributions estimated from 10 000 permutations (Jackson and Somers 1989).

To test for differences in emerging insect abundance ($\text{no. m}^{-2}\cdot\text{d}^{-1}$) and production ($\text{mg dry weight}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) among *P. angustifolia* genotypes and cross types, repeated measures MANOVA (rmMANOVA) tests were conducted in JMP Pro (SAS Institute Inc. 2013). Separate rmMANOVA tests were done for each response variable, including total abundance and production, abundance and production of dominant taxa, abundance and production of nonchironomid taxa, and abundance and production of functional feeding groups. For each rmMANOVA model, litter type (for either cross types or *P. angustifolia* genotypes) was the between-subjects factor and time was the within-subjects factor. We tested cross type litter and genotype litter separately because cross type litter represented mixtures of genotypes within the common garden (i.e., replication was of mixed litter for each cross type), whereas genotype-level litter represented individual genotypes that were not mixed (i.e., replication was from individual clones of each genotype). Both cross type and genotype were treated as fixed effects. Although treating genotype as a fixed effect limits our ability to generalize our findings, we used this approach because *P. angustifolia* genotypes were not chosen randomly, but to maximize litter phytochemical differences. We used rmMANOVA instead of traditional, univariate repeated-measures ANOVA (rmANOVA) for two reasons. First, rmMANOVA generally has more power to resolve differences compared to rmANOVA when sample sizes are reasonably large (Maxwell and Delaney 2004) and epsilon is low (Mendoza et al. 1974, Stevens 2012), which was generally the case for this study. Second, rmMANOVA is free of the assumption of sphericity (O'Brien and Kaiser 1985), which was violated for most of our data sets. Wilk's lambda was used as the test statistic for hypothesis testing in MANOVA. Species richness and diversity (Shannon's H') were all calculated in PC-ORD (McCune and

Mefford 2011) and data were analyzed using rmMANOVA, as described above. Abundance and production data were log-10 transformed and diversity data were arcsine-square-root transformed, when necessary, to meet the rmMANOVA assumption of normality.

Nonmetric multidimensional scaling (NMDS) ordinations were performed for genotype and cross type insect communities using PC-ORD with Bray–Curtis distances of relative abundances (e.g., the proportion of the maximum observed abundance for a given taxa). Multiresponse permutation procedures (MRPP) were used to make comparisons among groups, and indicator species analyses (ISA) (Dufrêne and Legendre 1997) were performed in PC-ORD to determine what species of insects differentiated among litter types.

Decomposition was modeled using exponential decay:

$$L_f = L_i e^{-kt}$$

where L_f was the AFDM of remaining litter at time t , L_i was the AFDM of initial litter from handling packs (as described by Benfield (2006)), and kd^{-1} was the instantaneous decomposition rate constant. Decomposition rate constants were compared among treatments using ANOVA in JMP Pro.

RESULTS

Genetic relationships with aquatic insect communities

Consistent with our first hypothesis, genetic similarity within *P. angustifolia* correlated with the community composition of emerging insects, such that litter from trees that were more closely related had more similar emerging insect communities (Fig. 2a). The correlation between genetic similarity and emerging insect community similarity for *P. angustifolia* genotypes was the strongest when insect abundances for all twelve harvest dates were used (Mantel $r = 0.57$, $P = 0.0045$). This pattern was not apparent when examining single harvests because of the high variability among replicates at any given sample date. Despite temporal variability, emerging insect communities over the entire 12-week study showed a clear relationship with tree genetic distance.

Relationships among genetic distance, litter traits, and emerging insect communities were nuanced. As predicted, within *P. angustifolia* genetic similarity significantly correlated with decomposition rate (partial Mantel $r = 0.76$, $P = 0.019$; Fig. 2a), which also correlated with the emerging insect community (partial Mantel $r = 0.76$, $P = 0.0062$; Fig. 2a). In addition, litter thickness (mm) and litter nitrogen (%) were significantly correlated with genetic similarity, and the litter fungal community was marginally correlated with genetic similarity. Only the litter fungal community was directly associated with the emerging insect community (Fig. 2a). Rather, litter thickness (mm), litter nitrogen (%), and the litter fungal community were correlated (%N was marginally significant) with decomposition rates (Fig. 2b), which was the strongest factor associated with the emerging insect community. In contrast to our initial predictions, genetically similar trees did not have similar litter lignin (%), condensed tannins (%), bulk density ($g\ L^{-1}$), or C:N ($gC\ gN^{-1}$), despite genetic control over many of these traits (Holeski et al. 2012, Busby et al. 2014), and none of these traits were significantly associated with either decomposition or the emerging insect community (Fig. 2a, b). However, in a separate analysis, lignin and condensed tannins were treated as a composite variable representing recalcitrant litter chemistry, and this composite variable was significantly correlated with the emerging insect community (partial Mantel $r = 0.37$, $P = 0.048$). The NMDS analysis was consistent with the Mantel tests and showed that emerging insect communities differentiated among litter of different *P. angustifolia* genotypes (MRPP: $A = 0.040$, $P = 0.0042$; Fig. 3a).

In contrast to genotype comparisons, differences among emerging insect communities of mixed cross type litter were not as pronounced. Though *P. angustifolia* and *P. fremontii* had, on average, distinct litter traits (Table 2), emerging insect communities were only marginally different among cross types (MRPP: $A = 0.035$, $P = 0.082$; Fig. 3b). In addition, communities associated with F_1 hybrid litter were very similar to those associated with *P. angustifolia* litter (MRPP: $A = 0.0030$, $P = 0.30$; Fig. 3b). Nine species differentiated among genotypes (five Diptera species, two Trichoptera species, one Ephemeroptera species, and one Coleoptera species), and three

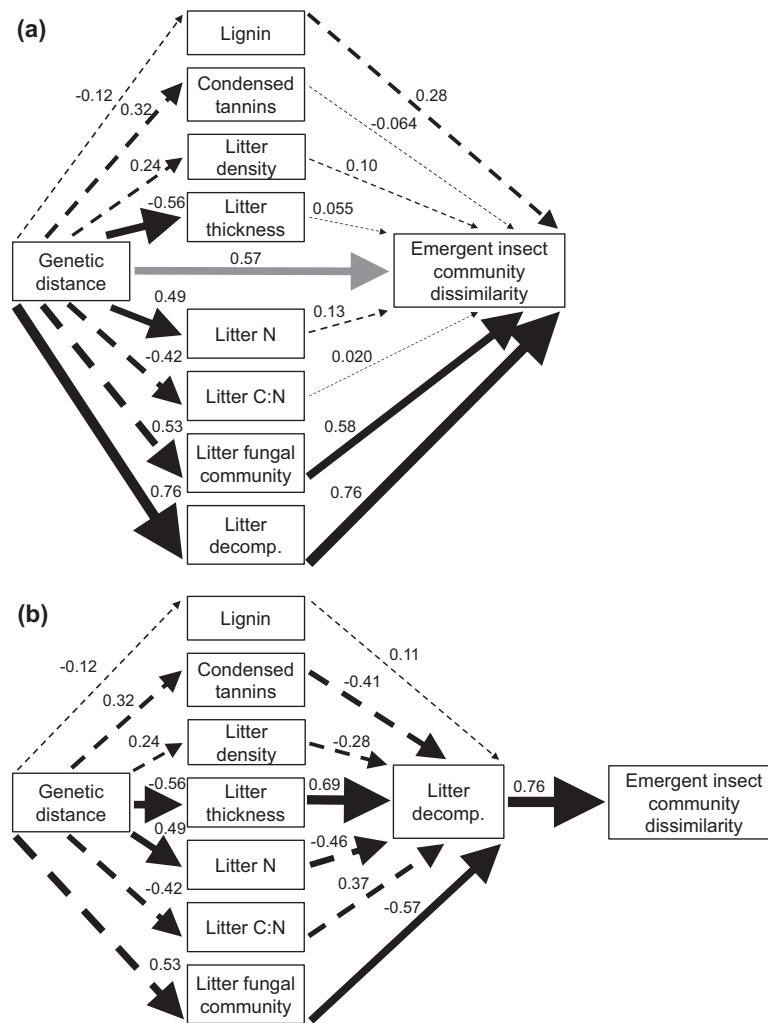


Fig. 2. Path diagrams of two ways plant genetic distance influences emerging aquatic insects: (a) through leaf litter traits that directly influence aquatic insects and (b) through leaf litter traits that influence decomposition, which was the main factor associated with aquatic insects. Arrows depict Mantel (gray) and partial-Mantel (black) correlations among plant genetic distance, emerging aquatic insect community dissimilarity, and litter traits, including lignin (%), condensed tannins (%), litter density (g L^{-1}), litter thickness (mm), litter nitrogen (%), litter C:N (gC gN^{-1}), litter fungal communities, and decomposition (k d^{-1}). Partial-Mantel correlations demonstrate associations between variables with the influence of all other variables factored out. Significant correlations are depicted by solid lines and non-significant correlations are depicted by dashed lines, with line thickness weighted based on Mantel or partial-Mantel r -values.

Diptera species discriminated among cross types (ISA: all $P < 0.05$). In summary, differences among litter types were less pronounced in the mixed cross type litter packs relative to single *P. angustifolia* genotype packs, even though the mixed packs represented a broader genetic comparison.

Contrary to our initial hypothesis, emerging insect abundance ($\text{no. m}^{-2}\cdot\text{d}^{-1}$) (rmMANOVA:

VA: $F_{1,88} = 0.32$, $P = 0.57$), production ($\text{mg dry weight}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) (rmMANOVA: $F_{1,88} = 0.026$, $P = 0.87$), species richness (rmMANOVA: $F_{1,88} = 2.0$, $P = 0.16$), and diversity (Shannon's H') (rmMANOVA: $F_{1,88} = 1.2$, $P = 0.28$) were not higher in mixed litter packs relative to single genotype packs. Restricting our comparisons to only *P. angustifolia* mixed litter treatments compared

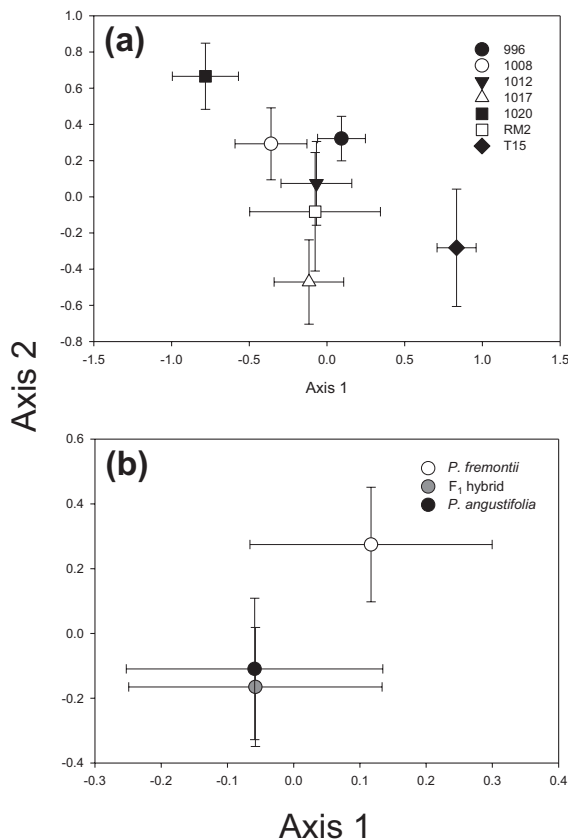


Fig. 3. Nonmetric multidimensional scaling (NMDS) ordination of emerging aquatic insects from packs containing leaf litter of (a) *Populus angustifolia* genotypes and (b) cottonwood cross types (*P. fremontii*, *P. angustifolia*, or F_1 hybrids).

to single genotype *P. angustifolia* treatments did not change these patterns (rmMANOVA: abundance: $F_{1,60} = 2.8$, $P = 0.098$; production: $F_{1,60} = 3.1$, $P = 0.086$; species richness: $F_{1,60} = 0.55$, $P = 0.46$; Shannon's H' : $F_{1,60} = 0.99$, $P = 0.32$). However, differences in community metrics were more pronounced among genotypes than cross types. *P. angustifolia* genotypes differed in emerging insect species richness (rmMANOVA: $F_{6,41} = 2.9$, $P = 0.020$), with the most species-rich genotype yielding, on average, 35% more species than the most species-poor genotype. Collectively, all seven genotypes yielded 42% more species than the average of the monocultures (species richness: all seven genotypes = 61, mean monoculture = 43 ± 1.4). Differences among genotypes in diversity varied with time (rmMANOVA:

Time \times Genotype: Shannon's H' : $F_{66,171.33} = 1.4$, $P = 0.0497$). There were no differences among cross type litter for these community metrics (rmMANOVA: all $P > 0.05$).

Emergence controlled by plant genotype and temporal variation

Total emerging insect abundance (no. $m^{-2} \cdot d^{-2}$) did not differ among litter of genotypes (rmMANOVA: $F_{6,41} = 0.37$, $P = 0.89$; Fig. 4a) or cross types (rmMANOVA: $F_{2,39} = 1.7$, $P = 0.20$; Fig. 4b). Genotypes, however, differed in the temporal pattern of total emerging insect abundance (rmMANOVA: Time \times Genotype: $F_{66,171.33} = 1.6$, $P = 0.0074$), but this was not the case for cross types (rmMANOVA: Time \times Cross type: $F_{22,58} = 1.3$, $P = 0.21$). Chironomids, small Diptera that can dominate assemblages (Jackson and Fisher 1986, Stagliano et al. 1998, Lynch et al. 2002), were the most abundant taxon in all litter packs (95% of emerging insect abundance and 78% of emerging insect production). When they were removed from the analysis, non-chironomid emerging insect abundance differed marginally among genotypes (rmMANOVA: $F_{6,41} = 2.1$, $P = 0.074$), with 56% higher abundance emerging from the highest compared to the lowest genotype, but there were no differences among cross types (rmMANOVA: $F_{2,39} = 1.8$, $P = 0.18$). In general, emerging insect production ($mg \cdot m^{-2} \cdot d^{-2}$) was more variable than abundance, and tended to not differ among genotypes (rmMANOVA: Genotype: $F_{6,41} = 0.61$, $P = 0.72$; Time \times Genotype: $F_{66,171.33} = 0.91$, $P = 0.67$) or cross types (rmMANOVA: Cross Type: $F_{2,39} = 2.1$, $P = 0.13$; Time \times Cross Type: $F_{22,58} = 0.99$, $P = 0.49$), though non-chironomid production tended to differ among genotypes (rmMANOVA: Genotype: $F_{6,41} = 1.9$, $P = 0.11$, 40% higher production from the highest compared to lowest genotype) and cross types through time (rmMANOVA: Time \times Cross Type: $F_{22,58} = 1.5$, $P = 0.11$). In addition, despite the strong influence of litter decomposition rates on the emergent insect community, univariate regressions relating litter decomposition to total abundance and production of emerging insects indicated consistent but weaker patterns for both cross type and genotype litter (i.e., all regressions were negative, but not significant, $P > 0.05$).

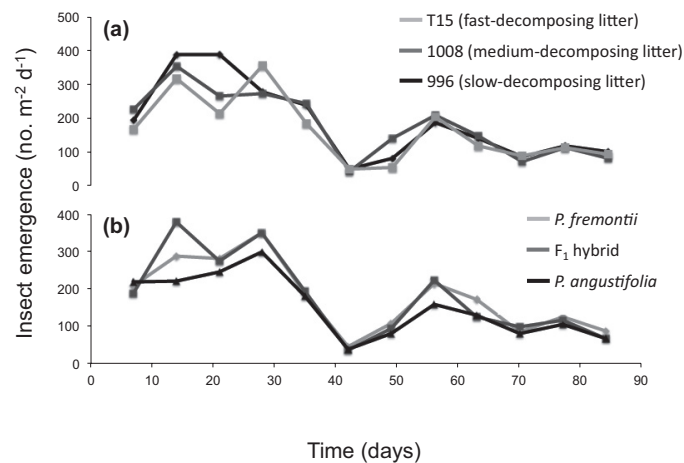


Fig. 4. Insect emergence (no. m⁻² d⁻¹) from packs containing leaf litter of (a) *Populus angustifolia* genotypes and (b) cottonwood cross types (*P. fremontii*, F₁ hybrid or *P. angustifolia*). For clarity, panel (a) only includes three genotypes, representing relatively fast- (T15), medium- (1008), and slow-decomposing (996) litter.

Emerging insect abundance (no. m⁻² d⁻²) and production (mg m⁻² d⁻²) of functional feeding groups and other taxonomic groups also discriminated more among litter of cottonwood genotypes than among cross types. Emerging Trichoptera abundance significantly differed among genotypes (rmMANOVA: $F_{6,41} = 2.5$, $P = 0.039$, 155% higher abundance from the highest compared to lowest genotype). Ephemeroptera (rmMANOVA: $F_{6,41} = 1.8$, $P = 0.012$), collector-filterer (rmMANOVA: $F_{6,41} = 2.1$, $P = 0.075$), and parasitoid (rmMANOVA: $F_{6,41} = 1.9$, $P = 0.11$) abundance tended to differ among genotypes. In addition, the effect of genotype on emerging shredder (rmMANOVA: Time \times Genotype: $F_{66,171.33} = 1.4$, $P = 0.052$) and collector-filterer (rmMANOVA: Time \times Genotype: $F_{66,171.33} = 1.5$, $P = 0.021$) abundance varied with time. Conversely, only emerging parasitoid abundance differed consistently among cross type litter (rmMANOVA: $F_{2,39} = 3.7$, $P = 0.034$, 69% and 26% higher production from F₁ compared to *P. fremontii* and *P. angustifolia* litter, respectively), and there was a time-dependent effect of cross type on emerging shredder abundance (rmMANOVA: Time \times Cross Type: $F_{22,58} = 1.8$, $P = 0.042$). No other taxa differed in emerging insect abundance among cross types. Emerging insect production differed among genotypes with time for both collector-filterers (rmMANOVA: Time \times Genotype: $F_{66,171.33} = 1.4$, $P = 0.044$) and Trichoptera taxa (rmMANOVA: Time \times Genotype: $F_{66,171.33} = 1.4$, $P = 0.041$). In ad-

dition, there was a trend toward predator production differing among genotypes (rmMANOVA: $F_{6,41} = 2.2$, $P = 0.058$, 29-times higher production from the highest compared to lowest genotype). Only collector-filterer production differed among cross type litter (rmMANOVA: $F_{2,39} = 3.8$, $P = 0.031$, 26% and 29% higher production from F₁ compared to *P. fremontii* and *P. angustifolia* litter, respectively), though there was a trend toward Ephemeroptera production differing among cross types (rmMANOVA: $F_{2,39} = 2.8$, $P = 0.075$). In summary, insect responses varied, but in general genotypic differences in litter resulted in differential rates of emerging insect abundance and production of multiple taxa and functional feeding groups, whereas responses to cross type mixtures were minimal.

DISCUSSION

The genetic footprint of terrestrial plants in aquatic ecosystems

Plant genotypes influence terrestrial litter invertebrate communities (Classen et al. 2006, Zytynska et al. 2011), though these effects have been postulated to be weaker in aquatic systems, where invertebrate communities do not necessarily discriminate among litter of different tree genotypes (LeRoy et al. 2007). Our results demonstrate that plant genotype effects are apparent for emerging aquatic insect communities,

bringing full circle the afterlife effects of plant genes on terrestrial-aquatic interactions (LeRoy et al. 2006, 2007, Lecerf and Chauvet 2008, Jackrel and Wootton 2014): the emerging insect communities are shaped by the genetic-based traits of the trees from the terrestrial environment to which aquatic insects return when they emerge from their aquatic life stage. This adds a genetic dimension to our understanding of terrestrial-aquatic linkages through reciprocal ecosystem subsidies (Likens and Bormann 1974, Nakano and Murakami 2001, Baxter et al. 2004).

Our findings also show that genotypes that are more similar to one another in their neutral molecular markers support more similar communities. This has also been found for canopy arthropods in temperate forests and rain forests (Bangert et al. 2006a, b, Barbour et al. 2009b, Zytynska et al. 2011, 2012, Ferrier et al. 2012). The correlations we report may be conservative as correlations between quantitative trait markers were nearly twice as high as those with neutral markers (Barbour et al. 2009b).

Implications of riparian tree clonality for headwater streams

The stronger response of the emerging insect community to litter from *P. angustifolia* genotypes than from mixtures of genotypes representing cross types could be because *P. angustifolia* genotypes were chosen to represent a wide range of phytochemical traits, whereas cross type litter was mixed, including multiple genotypes for a given litter type (*P. fremontii*, F₁ hybrid, and *P. fremontii*). Intraspecific variation in litter phytochemistry (Holeski et al. 2012) and litter decomposition (Lecerf and Chauvet 2008) can rival or exceed that of interspecific variation in these traits. This may explain why we observed differences among genotypes but not cross types in emerging insect communities: variation among the genotypes included in the mixed cross type litter packs likely muted differences in average decomposition and insect communities detectable for the cross type comparisons.

Aquatic insects had a higher fidelity to litter of *P. angustifolia* genotypes than to mixtures of cross types, possibly reflecting the clonal nature of *P. angustifolia* (Rood et al. 1994, Gom and Rood 1999) and its clumped distribution in southwestern headwater streams (Braatne et al. 1996).

Thus, in high gradient, low-order streams where leaf retention rates are high (Webster et al. 1994, Jones 1997) and litter does not travel far from its source, aquatic insects may experience large aggregates of litter from a single genotype. Oak Creek, AZ, has relatively high litter retention rates ($k = 0.061 \pm 0.0099 \text{ m}^{-1}$ for *Populus*, Z. Compson, unpublished data), especially for a stream of its size (Strahler stream order = 4), and so insect communities emerging from particular locations in this stream likely encounter one or a few genotypes in large patches of litter. Consequently, genotypic effects of leaf litter on aquatic insects and insect emergence might be magnified in this and other headwater streams, especially for slow-decomposing litter, which will remain in the stream longer and provide a longer temporal footprint. Because different genotypes supported different species richness, diversity through time, and community composition in our study, the phenomenon of litter patchiness in headwater streams (Casas 1997, Rowe and Richardson 2001, Kobayashi and Kagaya 2002) underscores the importance of maintaining riparian tree diversity.

Factors influencing aquatic insect emergence

Plant genetic similarity has been proposed to influence the community similarity of associated organisms through litter chemistry (Legendre 1993, Bangert et al. 2006b). Our study demonstrated that recalcitrant litter chemistry was strongly associated with the emerging insect community among *P. angustifolia* genotypes, but only when it was treated as a composite variable: when lignin and condensed tannins were treated separately, they did not have significant influences on the emerging insect community. This suggests that litter chemistry, including other litter chemistry variables not measured in this study (e.g., salicortin), functions as a multivariate trait (sensu Holeski et al. 2012) to influence the emerging insect community. Litter chemistry itself was not associated with genetic distance. Rather, the influence of plant genetic similarity on community similarity of emerging insects was through litter decomposition rate, which was itself influenced by litter thickness, litter N, and litter fungal communities. With the growing number of studies demonstrating intraspecific variation in aquatic litter decomposition in the cottonwood system and

elsewhere (Lecerf and Chauvet 2008, Jackrel and Wootton 2014), these results could mean that aquatic litter communities are more sensitive to plant genetic identity than once thought. Possible explanations for the association between terrestrial fungal pathogens and aquatic insects are that the terrestrial fungi are retained and provide a food source for insects, or litter traits that promote terrestrial fungi may also induce higher colonization of aquatic fungi.

In our study, litter from *Populus* cross types and *P. angustifolia* genotypes with slower decomposition rates tended to yield higher emerging insect abundance and production (all univariate correlations negative, but $P > 0.05$ for all). While laboratory preference experiments generally demonstrate a preference of shredders for more labile leaf litter (Graça 2001, and references therein), other aquatic insects use leaf litter as a habitat or substrate that collects fine particulate detritus (Richardson 1992); this, coupled with the fact that aquatic insects can both contribute to and be affected by litter decomposition complicates the causal linkage between litter decomposition and insect emergence. Recalcitrant litter decomposes slowly and slows down the decomposition of labile leaf litter in mixtures (Swan and Palmer 2004), likely imparting stability by extending the availability of other more labile resources (Palmer et al. 2000) to the many stream invertebrates relying on terrestrial litter subsidies for food (Cummins et al. 1989, Richardson 1991, 1992) and habitat (Reice 1978, Richardson 1992). Therefore, litter mixtures including genotypes that have very recalcitrant litter will likely lead to a more sustained resource pulse lasting later into the year. As recalcitrant litter has been associated with more spring-summer shredders (Grubbs and Cummins 1994) and higher insect emergence rates (Kominoski et al. 2012, Compson et al. 2013), the presence of recalcitrant litter in streams could also mean a longer, more sustained pulse of emerging insects to fish and riparian predators (Baxter et al. 2005).

Implications of differential responses of emergent insect groups

The finding that many groups of emerging aquatic insects that do not directly feed on leaf litter (e.g., Ephemeroptera, collector-filterers, parasitoids) discriminated among litter types

while shredders generally did not (except in the context of temporal dynamics) could have arisen for several reasons. For example, litter decomposition dynamics might have caused a tradeoff for shredders, such that fast-decomposing litter was more palatable and accessible, but disappeared more quickly, than slow-decomposing litter, which remained in the stream longer and provided more structural integrity for habitat. Conversely, taxa that do not need litter as a food source would not have been affected by the resource-habitat tradeoff, being driven instead by the structural aspects of leaf litter and thus choosing litter types that provide more habitat for a longer time (e.g., litter from more recalcitrant *P. angustifolia* genotypes). Another possible explanation for the lack of differences in shredders among our litter types is shredder-predator interactions. While shredders have been shown to utilize leaf litter more for a food source than for habitat (Richardson 1992), selecting more labile, palatable litter types (Graça 2001, and references therein), in our study predator production was generally higher on fast-decomposing genotypes (e.g., T15, a fast-decomposing genotype, had 2.3 and 5.3 times higher predator production than the two slowest-decomposing genotypes, respectively). Predators, which can decrease litter decomposition by reducing detritivore abundance (Ruetz et al. 2002) or altering detritivore foraging behavior (Short and Holomuzki 1992), might have dampened shredder emergence from fast-decomposing litter through direct predation or by altering shredder behavior, causing them to forage less and develop more slowly or to choose to emerge outside of litter packs. In addition, shredders associated with slow-decomposing litter might have benefitted from the added habitat complexity of the litter, providing them with a refuge from predation.

Temporal influences on insect emergence

Aquatic insect emergence varied through time, likely reflecting the influence of temperature, flow, and taxon-specific behavior, all known to affect the timing of emergence (Power and Rainey 2000, Iwata 2003, Power et al. 2004, Baxter et al. 2005). No single date yielded strong patterns, underscoring the importance of multiple sampling events to characterize emergence (Judd

1962, Harper 1978, Nakano and Murakami 2001). Despite the temporal variability in our study, the association between *P. angustifolia* genetic similarity and emerging insect community similarity strengthened as more sampling dates were aggregated, suggesting persistent afterlife effects of plant genes on insect communities.

Temporal variation is common for insect emergence in aquatic systems. Emergence can be continuous, rhythmic with a lunar period, sporadic (irregular intervals of a few days), or seasonal (Corbet 1964), and this varies among ecosystems (Corbet 1964, Sweeney and Vannote 1982). Litter quantity has been shown to influence the development time, survival, and traits influencing the vectorial capacity of mosquitoes (Araújo et al. 2012). Our results demonstrate that the genotype of leaf litter can influence the abundance and production of functionally important emerging insect groups and that these patterns can change through time. This suggests that the loss of riparian plant genotypes could alter the timing of aquatic insect emergence, which can influence the fitness of riparian predators (Sabo and Power 2002). Our finding that different genotypes promoted emergence at different times implies that the loss of riparian genotypes could disrupt the sustained seasonal pulse of aquatic insects to riparian predators, which depend on emerging insects from streams when terrestrial prey abundances are low (Nakano and Murakami 2001). Thus, the genetic identity of leaf litter, by influencing secondary production and insect emergence, in turn could affect the productivity and fitness of riparian predators.

Another temporal aspect to aquatic insect emergence that could have important ecosystem implications is differential turnover and development times of insects feeding on different litter types. Because leaf litter from different genotypes supports different communities of emerging insects, this could affect the total rate of emergence through dominance of nonemerging or long time-to-emergence insects. The loss of litter through time prevented us from running our experiment longer than 3 months, which could have prevented us from detecting many slowly developing, predatory taxa, like Zygoptera and Anisoptera. Still, we demonstrated a trend for different genotypes supporting different emerging predator production. Shifts in community composition between

commonly emerging or fast-developing forms to a community dominated by non-emerging or slow-developing taxa would have important implications for the subsidy pulse to terrestrial systems. For example, differences in development time between detritivores and predators can lead to accelerated nutrient cycling in the presence of predators, which can convert the mobile (via emergence) pool of N in detritivores into fecal pellets that act as a sink for N for the local ecosystem (Ngai and Srivastava 2006). In addition, predators are particularly important in controlling cross-ecosystem linkages because they create strong species interactions that reverberate across ecosystems, affecting landscape-level processes and driving local species interactions (Knight et al. 2005).

Restoration implications

Understanding ecosystem-level consequences of losing genetic diversity in the riparian zone will be important for land managers who are spending billions of dollars on river restoration projects across North America (Bernhardt et al. 2005), including large investments in restoring buffer zones around streams (Balana et al. 2012, Newton 2012, Stutter et al. 2012). Because genetically similar genotypes of *P. angustifolia* cottonwoods support similar emerging insect communities, loss of riparian genetic diversity, especially genetically dissimilar genotypes, will likely negatively impact aquatic insect diversity. In our study, the species richness of a single *P. angustifolia* genotype ranged from 39 to 49 (mean: 43 ± 1.4), whereas species richness across all seven genotypes together was 61. Thus, a riparian corridor planted with clumps of seven different genotypes would support an emerging aquatic insect community with 42% more insect species compared to a monoculture. This added diversity could influence ecosystem processes, like decomposition (Swan and Palmer 2004), reflecting the sensitivity of detritivores to cross-habitat resource subsidies (Marczak et al. 2007). In addition, our results suggest that, if riparian tree genotypes that are genetically dissimilar are lost, there might be disproportionately large losses in aquatic insect diversity. Thus, restoration aiming to promote aquatic biodiversity should not only consider riparian tree genetic diversity, but also prioritize maximizing genetically dissimilar genotypes in the riparian zone.

ACKNOWLEDGMENTS

Z. G. Compson, K. J. Adams, B. A. Hungate, T. G. Whitham, and J. C. Marks designed the study. Z. G. Compson, K. J. Adams, and T. Wojtowicz collected field data. Z. G. Compson, K. J. Adams, A. C. Ford, and several undergraduate student technicians sorted and identified insects. T. G. Whitham designed and maintained the common garden. N. Meneses conducted genetics work and calculated genetic distances, and P. E. Busby collected fungal community data and calculated associated metrics. Z. G. Compson analyzed the data and wrote the first draft of the manuscript; all authors contributed to manuscript revisions. We thank Greg Florian of the Northern Arizona University Machine Shop for assistance with designing and constructing large litter packs, emergence nets, and insect collectors. Heather Provincio, District Ranger of the Redrock Ranger District, granted access to our field site and assisted with efforts to interpret our study to the public and prevent vandalism while the experiment took place. We also thank many friends who volunteered to help with field work, including Eric Retterbush, Rita Greenwell, and Michael Barger. This manuscript benefitted greatly from discussions with members of the Cottonwood Ecology Group, the Merriam-Powell Center for Environmental Research, and the Center for Ecosystem Science and Society. Funding was provided by NSF through the Ecosystem Studies (DEB-1120343), IGERT (DGE-0549505), MRI (DBI-1126840), and FIBR (DEB-0425908) research programs. The grant is NSF Dimensions grant DEB-1321792.

LITERATURE CITED

- Applied Biosystems. 2006. GeneMapper. Version 4.0. Applied Biosystems, Foster City, California, USA.
- Araújo, M. S., L. H. S. Gil and A. A. e-Silva. 2012. Larval food quantity affects development time, survival and adult biological traits that influence the vectorial capacity of *Anopheles darlingi* under laboratory conditions. *Malaria Journal* 11:261.
- Bain, M. B., A. L. Harig, D. P. Loucks, R. R. Goforth, and K. E. Mills. 2000. Aquatic ecosystem protection and restoration: advances in methods for assessment and evaluation. *Environmental Science and Policy* 3:89–98.
- Balana, B. B., M. Lago, N. Baggaley, M. Castellazzi, J. Sample, M. Stutter, B. Slee, and A. Vinten. 2012. Integrating economic and biophysical data in assessing cost-effectiveness of buffer strip placement. *Journal of Environmental Quality* 41:380–388.
- Bangert, R. K., G. J. Allan, R. J. Turek, G. M. Wimp, N. Meneses, G. D. Martinsen, P. Keim, and T. G. Whitham. 2006a. From genes to geography: a genetic similarity rule for arthropod community structure at multiple geographic scales. *Molecular Ecology* 15:4215–4228.
- Bangert, R. K., et al. 2006b. A genetic similarity rule determines arthropod community structure. *Molecular Ecology* 15:1379–1391.
- Barbour, R. C., S. C. Baker, J. M. O'Reilly-Wapstra, T. M. Harvest, and B. M. Potts. 2009a. A footprint of tree-genetics on the biota of the forest floor. *Oikos* 118:1917–1923.
- Barbour, R. C., J. M. O'Reilly-Wapstra, D. W. De Little, G. J. Jordan, D. A. Steane, J. R. Humphreys, J. K. Bailey, T. G. Whitham, and B. M. Potts. 2009b. A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology* 90:1762–1772.
- Barclay, R. M. R. 1991. Population-structure of temperate zone insectivorous bats in relation to foraging behavior and energy demand. *Journal of Animal Ecology* 60:165–178.
- Basaguren, A., and J. Pozo. 1994. Leaf litter processing of alder and eucalyptus in the Agüera stream system (Northern Spain). II: Macroinvertebrates associated. *Archiv für Hydrobiologie* 132:57–68.
- Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Nonnative stream fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85:2656–2663.
- Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201–220.
- Benfield, E. F. 2006. Decomposition of leaf material. Pages 125–155 in F. R. Hauer and G. A. Lamberti, editors. *Methods in stream ecology*, second edition. Academic Press, Burlington, Massachusetts, USA.
- Benjamin, J. R., K. D. Fausch, and C. V. Baxter. 2011. Species replacement by a nonnative salmonid alters ecosystem function by reducing prey subsidies that support riparian spiders. *Oecologia* 167:503–512.
- Bernhardt, E. S., et al. 2005. Synthesizing U.S. river restoration efforts. *Science* 308:636–637.
- Braatne, J. H., S. B. Rood, and P. E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. Pages 57–85 in R. F. Stettler, H. D. Bradshaw Jr., P. E. Heilman and T. M. Hinckley, editors. *Biology of Populus and its Implications for Management and Conservation*. NRC Research Press, Ottawa, Ontario, Canada.
- Briers, R. A., and J. H. Gee. 2004. Riparian forestry management and adult stream insects. *Hydrology and Earth System Sciences Discussions* 8:545–549.

- Briers, R. A., H. M. Cariss, and J. H. Gee. 2002. Dispersal of adult stoneflies (*Plecoptera*) from upland streams draining catchments with contrasting land-use. *Archiv für Hydrobiologie* 155:627–644.
- Busby, P. E., G. Newcombe, R. Dirzo, and T. G. Whitham. 2013. Genetic basis of pathogen community structure for foundation tree species in a common garden and in the wild. *Journal of Ecology* 101:867–877.
- Busby, P. E., G. Newcombe, R. Dirzo, and T. G. Whitham. 2014. Differentiating genetic and environmental drivers of plant-pathogen community interactions. *Journal of Ecology* 102:1300–1309.
- Canhoto, C. and M. A. S. Graça. 1992. Importância das folhas de eucalipto na alimentação de detritívoros aquáticos em ribeiros da zona centro de Portugal. *Actas do V Congresso Ibérico de Entomologia* 1:473–482.
- Canhoto, C. and M. A. S. Graça. 1995. Food value of introduced eucalypt leaves for a Mediterranean stream detritivore: *Tipula lateralis*. *Freshwater Biology* 34:209–214.
- Casas, J. J. 1997. Invertebrate assemblages associated with plant debris in a backwater of a mountain stream: natural leaf packs vs. debris dam. *Journal of Freshwater Ecology* 12:39–49.
- Classen, A. T., J. DeMarco, S. C. Hart, T. G. Whitham, N. S. Cobb, and G. W. Koch. 2006. Impacts of herbivorous insects on decomposer communities during the early stages of primary succession in a semi-arid woodland. *Soil Biology and Biochemistry* 38:972–982.
- Cohen, J. S., J. C. Maerz, and B. Blossey. 2012. Traits, not origin, explain impacts of plants on larval amphibians. *Ecological Applications* 22:218–228.
- Collier, K. J., B. J. Smith, and B. R. Baillie. 1997. Summer light-trap catches of adult Trichoptera in hill-country catchments of contrasting land use, Waikato, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31:623–634.
- Compson, Z. G., M. Z. Mier, and J. C. Marks. 2009. Effects of travertine and flow on leaf retention in Fossil Creek, Arizona. *Hydrobiologia* 630:187–197.
- Compson, Z. G., K. J. Adams, J. A. Edwards, J. M. Maestas, T. G. Whitham, and J. C. Marks. 2013. Leaf litter quality affects aquatic insect emergence: contrasting patterns from two foundation trees. *Oecologia* 173:507–519.
- Compson, Z. G., B. A. Hungate, G. W. Koch, S. C. Hart, J. M. Maestas, K. J. Adams, T. G. Whitham, and J. C. Marks. 2015. Closely related tree species differentially influence the transfer of carbon and nitrogen from leaf litter up the aquatic food web. *Ecosystems* 18:186–201.
- Corbet, P. S. 1964. Temporal patterns of emergence in aquatic insects. *Canadian Entomologist* 96:264–279.
- Cornwell, W. K., et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11:1065–1071.
- Crutsinger, G. M., M. D. Collins, J. A. Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313:966–968.
- Crutsinger, G. M., W. N. Reynolds, A. T. Classen, and N. J. Sanders. 2008. Disparate effects of plant genotypic diversity on foliage and litter arthropod communities. *Oecologia* 158:65–75.
- Crutsinger, G. M., S. Y. Strauss and J. A. Rudgers. 2010. Genetic variation within a dominant shrub species determines plant species colonization in a coastal dune ecosystem. *Ecology* 91:1237–1243.
- Cummins, K. W., M. A. Wiltzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989. Shredders and riparian vegetation: leaf litter that falls into streams influences communities of stream invertebrates. *BioScience* 39:24–31.
- Dirzo, R., and C. Domínguez. 1995. Plant-animal interactions in Mesoamerican tropical dry forests. Pages 304–325 in S. H. Bullock, H. A. Mooney and E. Medina, editors. *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, UK.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.
- Dungey, H. S., B. M. Potts, T. G. Whitham, and H. F. Li. 2000. Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. *Evolution* 54:1938–1946.
- Ferrier, S. M., R. K. Bangert, E. I. Hersch-Green, J. K. Bailey, G. J. Allan, and T. G. Whitham. 2012. Unique arthropod communities on different host-plant genotypes results in greater arthropod diversity. *Arthropod-Plant Interactions* 6:187–195.
- Findlay, S., M. Carreiro, V. Krischik, and C. G. Jones. 1996. Effects of damage to living plants on leaf litter quality. *Ecological Applications* 6:269–275.
- Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43:421–439.
- Fritz, R. S., and P. W. Price. 1988. Genetic variation among plants and insect community structure: willows and sawflies. *Ecology* 69:845–856.
- Gom, L. A., and S. B. Rood. 1999. Patterns of clonal occurrence in a mature cottonwood grove along the

- Oldman River, Alberta. *Canadian Journal of Botany* 77:1095–1105.
- Goslee, S. C., and D. L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22:1–19.
- Graça, M. A. S. 2001. The role of invertebrates on leaf litter decomposition in streams—a review. *International Review of Hydrobiology* 86:383–393.
- Gray, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. *American Midland Naturalist* 129:288–300.
- Greig, H. S., P. Kratina, P. L. Thompson, W. J. Palen, J. S. Richardson, and J. B. Shurin. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. *Global Change Biology* 18:504–514.
- Grimm, N. B. 1987. Nitrogen dynamics during succession in a desert stream. *Ecology* 68:1157–1170.
- Grubbs, S. A., and K. W. Cummins. 1994. Processing and macroinvertebrate colonization of black cherry (*Prunus serotina*) leaves in two streams differing in summer biota, thermal regime and riparian vegetation. *American Midland Naturalist* 132:284–293.
- Harper, P. P. 1978. Variations in the production of emerging stream insects from a Quebec stream. *Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen* 20:1317–1323.
- Harrison, S. S. C., and I. T. Harris. 2002. The effects of bankside management on chalk stream invertebrate communities. *Freshwater Biology* 47:2233–2245.
- Holeski, L. M., M. L. Hillstrom, T. G. Whitham, and R. L. Lindroth. 2012. Relative importance of genetic, ontogenetic, induction, and seasonal variation in producing a multivariate defense phenotype in a foundation tree species. *Oecologia* 170:695–707.
- Hoover, T. M., J. S. Richardson, and N. Yonemitsu. 2006. Flow-substrate interactions create and mediate leaf litter resource patches in streams. *Freshwater Biology* 51:435–447.
- Hulberg, L. W., and J. S. Oliver. 1980. Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1130–1139.
- Hynes, H. B. N. 1975. The stream and its valley. *Verhandlungen des Internationalen Verein Limnologie* 19:1–15.
- Iwata, T. 2003. The roles of fluvial geomorphology in the trophic flow from stream to forest ecosystems. Dissertation. Kyoto University, Kyoto, Japan.
- Jackrel, S. L., and J. T. Wootton. 2014. Local adaptation of stream communities to intraspecific variation in a terrestrial ecosystem subsidy. *Ecology* 95:37–43.
- Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology* 67:629–638.
- Jackson, D. A., and K. M. Somers. 1989. Are probability estimates from the permutation model of Mantel's test stable? *Canadian Journal of Zoology* 67:766–769.
- Johnson, M. T. J., M. J. Lajeunesse, and A. A. Agrawal. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* 9:24–34.
- Jones, J. B. Jr. 1997. Benthic organic matter storage in streams: influence of detrital import and export, retention mechanisms, and climate. *Journal of the North American Benthological Society* 16:109–119.
- de Jong, J. and I. Ahlén. 1991. Factors affecting the distribution pattern of bats in Uppland, Central Sweden. *Holarctic Ecology* 14:92–96.
- Judd, W. W. 1962. A study of the population of insects emerging as adults from Medway Creek at Arva, Ontario. *American Midland Naturalist* 68:463–473.
- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. *Nature* 437:880–883.
- Kobayashi, S., and T. Kagaya. 2002. Differences in litter characteristics and macroinvertebrate assemblages between litter patches in pools and riffles in a headwater stream. *Limnology* 3:37–42.
- Kohler, S. L., and M. J. Wiley. 1997. Pathogen outbreaks reveal large-scale effects of competition in stream communities. *Ecology* 78:2164–2176.
- Kominoski, J. S., S. Larranaga, and J. S. Richardson. 2012. Invertebrate feeding and emergence timing vary among streams along a gradient of riparian forest composition. *Freshwater Biology* 57:759–772.
- Lamit, L. J., M. A. Bowker, L. M. Holeski, R. R. Næsborg, S. C. Wooley, M. Zinkgraf, R. L. Lindroth, T. G. Whitham, and C. A. Gehring. 2011. Genetically-based trait variation within a foundation tree species influences a dominant bark lichen. *Fungal Ecology* 4:103–109.
- Lecerf, A., and E. Chauvet. 2008. Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology* 9:598–605.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.
- Lenat, D. R. 1988. Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. *Journal of the North American Benthological Society* 7:222–233.
- LeRoy, C. J., T. G. Whitham, P. Keim, and J. C. Marks. 2006. Plant genes link forests and streams. *Ecology* 87:255–261.

- LeRoy, C. J., T. G. Whitham, S. C. Wooley, and J. C. Marks. 2007. Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river. *Journal of the North American Benthological Society* 26:426–438.
- Likens, G. E., and F. H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. *BioScience* 24:447–456.
- Lindroth, R. L., M. T. S. Hsia, and J. M. Scriber. 1987. Seasonal patterns in the phytochemistry of three *Populus* species. *Biochemical Systematics and Ecology* 15:681–686.
- Lynch, R. J., S. E. Bunn, and C. P. Catterall. 2002. Adult aquatic insects: potential contributors to riparian food webs in Australia's wet-dry tropics. *Austral Ecology* 27:515–526.
- Malmqvist, B., and D. Oberle. 1995. Macroinvertebrate effects on leaf pack decomposition in a lake outlet stream in northern Sweden. *Nordic Journal of Freshwater Research* 70:12–20.
- Marczak, J. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: tropic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140–148.
- Maxwell, S. E., and H. D. Delaney. 2004. *Designing experiments and analyzing data: a model comparison perspective*, second edition. Psychology Press, New York, New York, USA.
- McCune, B. and M. J. Mefford. 2011. PC-ORD. Multivariate analysis of ecological data. Version 6. MjM Software, Gleneden Beach, Oregon, USA.
- McCune, B., J. B. Grace, and D. L. Urban. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon, USA.
- McIntosh, A. R. 2000. Aquatic predator-prey interactions. Pages 125–155 in K. J. Collier and M. J. Winterbourn, editors. *New Zealand stream invertebrates: ecology and implications for management*. New Zealand Limnological Society, Christchurch, New Zealand.
- Mendoza, J. L., L. E. Toothaker, and W. A. Nicewander. 1974. A Monte Carlo comparison of the univariate and multivariate methods for the groups by trials repeated measures design. *Multivariate Behavioral Research* 9:165–177.
- Merritt, R. W., and K. W. Cummins, editors. 1996. *An introduction to the aquatic insects of North America*. Kendall Hunt, Dubuque, Iowa, USA.
- Meyer, J. L., J. B. Wallace, and S. L. Eggert. 1998. Leaf litter as a source of dissolved organic carbon in streams. *Ecosystems* 1:240–249.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Science* 98:166–170.
- Newton, G. 2012. Buffer zones for aquatic biodiversity conservation. *Australasian Plant Conservation: Journal of the Australian Network for Plant Conservation* 21:18–22.
- Ngai, J. T., and D. S. Srivastava. 2006. Predators accelerate nutrient cycling in a bromeliad ecosystem. *Science* 314:963.
- Nolen, J. A., and R. G. Pearson. 1993. Factors affecting litter processing by *Anisocentropus kirramus* (Trichoptera: Calamoceratidae) from an Australian tropical rainforest stream. *Freshwater Biology* 29:469–479.
- O'Brien, R. G., and M. K. Kaiser. 1985. MANOVA method for analyzing repeated measures designs: an extensive primer. *Psychological Bulletin* 97:316–333.
- Paetzold, A., C. J. Schubert, and K. Tockner. 2005. Aquatic-terrestrial linkages along a braided river: riparian arthropods feeding on aquatic insects. *Ecosystems* 8:748–759.
- Palmer, M. A., et al. 2000. Linkages between aquatic sediment biota and life above sediments as potential drivers of biodiversity and ecological processes. *BioScience* 50:1062–1075.
- Palo, R. T. 1984. Distribution of birch (*Betula* spp.), willow (*Salix* spp.), and poplar (*Populus* spp.) secondary metabolites and their potential role as chemical defense against herbivores. *Journal of Chemical Ecology* 10:499–520.
- Peakall, R., and P. E. Smouse. 2006. GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6:288–295.
- Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics* 28:2537–2539.
- Peckarsky, B. L. 1985. Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? *Canadian Journal of Zoology* 63:1519–1530.
- Plafkin, J. L., M. T. Barbour, K. D. Porter, S. K. Gross and R. M. Hughes. 1989. Rapid bioassessment protocols for use in streams and rivers: benthic macroinvertebrates and fish. EPA/440/4-89/001. Environmental Protection Agency, Washington, DC, USA.
- Porter, L. J., L. N. Hrstich, and B. G. Chan. 1986. The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. *Phytochemistry* 25:223–230.
- Power, M. E., and W. E. Rainey. 2000. Food webs and resource sheds: towards spatially delimiting trophic interactions. Pages 291–314 in M. J. Hutchings, E. A. John and A. J. A. Stewart, editors. *Ecological consequences of habitat heterogeneity*. Blackwell, Oxford, England.
- Power, M. E., W. E. Rainey, M. S. Parker, J. L. Sabo, A. Smyth, S. Khandwala, J. C. Finlay, F. C. McNeely, K.

- Marsee, and C. Anderson. 2004. River to watershed subsidies in an old-growth conifer forest. Pages 217–240 in G. A. Polis, M. E. Power and G. Huxel, editors. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois, USA.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rehill, B. J., A. Clauss, L. Wiczorek, T. G. Whitham, and R. L. Lindroth. 2005. Foliar phenolic glycosides from *Populus fremontii*, *Populus angustifolia*, and their hybrids. *Biochemical Systematics and Ecology* 33:125–131.
- Rehill, B. J., T. G. Whitham, G. D. Martinsen, J. A. Schweitzer, J. K. Bailey, and R. L. Lindroth. 2006. Developmental trajectories in cottonwood phytochemistry. *Journal of Chemical Ecology* 32:2269–2285.
- Reice, S. R. 1978. The role of detritivore selectivity in species-specific litter decomposition in a woodland stream. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 20:1396–1400.
- Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology* 72:873–887.
- Richardson, J. S. 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshwater Biology* 27:169–176.
- Rood, S. B., C. Hillman, T. Sanche, and J. M. Mahoney. 1994. Clonal reproduction of riparian cottonwoods in southern Alberta. *Canadian Journal of Botany* 72:1766–1774.
- Rowe, L., and J. S. Richardson. 2001. Community responses to experimental food depletion: resource tracking by stream invertebrates. *Oecologia* 129:473–480.
- Ruetz, C. R., R. M. Newman, and B. Vondracek. 2002. Top-down control in a detritus-based food web: fish, shredders, and leaf breakdown. *Oecologia* 132:307–315.
- Sabo, J. L., and M. E. Power. 2002. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology* 83:1860–1869.
- Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society* 21:336–343.
- Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. *American Midland Naturalist* 129:234–240.
- Sanzone, D. M., J. L. Meyer, E. Marti, E. P. Gardiner, J. L. Tank JL and N. B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia* 134:238–250.
- SAS Institute Inc. 2013. JMP Pro. Version 11.0 SAS Institute Inc., Cary, North Carolina, USA.
- Schulze, D. J., and K. F. Walker. 1997. Riparian eucalypts and willows and their significance for aquatic invertebrates in the River Murray, South Australia. *Regulated Rivers: Research and Management* 13:557–577.
- Schweitzer, J. A., J. K. Bailey, S. C. Hart, G. M. Wimp, S. K. Chapman, and T. G. Whitham. 2005. The interaction of plant genotype and herbivory decelerate leaf litter decomposition and alter nutrient dynamics. *Oikos* 110:133–145.
- Schweitzer, J. A., J. K. Bailey, D. G. Fischer, C. J. LeRoy, E. V. Lonsdorf, T. G. Whitham, and S. C. Hart. 2008. Plant-soil-microorganism interactions: heritable relationships between plant genotype and associated soil microorganisms. *Ecology* 89:773–781.
- Short, T. M., and J. R. Holomuzki. 1992. Indirect effects of fish on foraging behaviour and leaf processing by the isopod *Lirceus fontinalis*. *Freshwater Biology* 27:91–97.
- Stagliano, D. M., A. C. Benke, and D. H. Anderson. 1998. Emergence of aquatic insects from 2 habitats in a small wetland of the southeastern USA: temporal patterns of numbers and biomass. *Journal of the North American Benthological Society* 17:37–53.
- Stevens, J. P. 2012. Applied multivariate statistics for the social sciences. Routledge, New York, New York, USA.
- Stoler, A. B., and R. A. Relyea. 2013. Leaf litter quality induces morphological and developmental changes in larval amphibians. *Ecology* 94:1594–1603.
- Stutter, M. I., W. J. Chardon, and B. Kronvang. 2012. Riparian buffer strips as a multifunctional management tool in agricultural landscapes: introduction. *Journal of Environmental Quality* 41:297–303.
- Sullivan, C. M., C. B. Shiel, C. M. McAney, and J. S. Fairley. 1993. Analysis of the diets of Leisler's *Nyctalus leisleri*, Daubenton's *Myotis daubentonii*, and pipistrelle *Pipistrellus pipistrellus* bats in Ireland. *Journal of Zoology* 231:656–663.
- Swan, C. M., and M. A. Palmer. 2004. Leaf diversity alters litter breakdown in a Piedmont stream. *Journal of the North American Benthological Society* 23:15–28.
- Sweeney, B. W., and R. L. Vannote. 1982. Population synchrony in mayflies: a predator satiation hypothesis. *Evolution* 36:810–821.
- Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Enkirekin, and M. L. Stephen. 2010. A review of alloch-

- thonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society* 29:118–146.
- Tuskan, G. A., L. E. Gunter, Z. K. Yang, T. M. Yin, M. M. Sewell, and S. P. DiFazio. 2004. Characterization of microsatellites revealed by genomic sequencing of *Populus trichocarpa*. *Canadian Journal of Forest Research* 34:85–93.
- Van Zandt, P. A., and A. A. Agrawal. 2004. Community-wide impacts of herbivore-induced plant responses in milkweed (*Asclepias syriaca*). *Ecology* 85:2616–2629.
- Wallace, J. B., M. R. Whiles, S. Eggert, T. F. Cuffney, G. J. Lugthart, and K. Chung. 1995. Long-term dynamics of coarse particulate organic matter in three Appalachian Mountain streams. *Journal of the North American Benthological Society* 14:217–232.
- Webster, J. R. and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567–594.
- Webster, J. R., and J. L. Meyer. 1997. Organic matter budgets for streams: a synthesis. *Journal of the North American Benthological Society* 16:141–161.
- Webster, J. R., A. P. Covich, J. L. Tank, and T. V. Crockett. 1994. Retention of coarse organic particles in streams in the southern Appalachian mountains. *Journal of the North American Benthological Society* 13:140–150.
- Webster, J. R., J. B. Wallace, and E. F. Benfield. 1995. Organic processes in streams of the eastern United States. Pages 117–187 in C. E. Cushing, K. W. Cummins and G. W. Minshall, editors. *Ecosystems of the world*. Elsevier, New York, New York, USA.
- Webster, J. R., E. F. Benfield, T. P. Ehrman, M. A. Schaeffer, J. L. Tank, J. J. Hutchens and D. J. D'angelo. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta Freshwater Biology 41:687–705.
- Wesner, J. S. 2010. Aquatic predation alters a terrestrial prey subsidy. *Ecology* 91:1435–1444.
- Whitham, T. G., et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* 7:510–523.
- Whitham, T. G., C. A. Gehring, L. J. Lamit, T. Wojtowicz, L. M. Evans, A. R. Keith, and D. S. Smith. 2012. Community specificity: life and afterlife effects of genes. *Trends in Plant Science* 17:271–281.
- Winterbourn, M. J., W. L. Chadderton, S. A. Entrekin, J. L. Tank, and J. S. Harding. 2007. Distribution and dispersal of adult stream insects in a heterogeneous montane environment. *Fundamental and Applied Limnology* 168:127–135.
- Wojtowicz, T., Z. G. Compson, L. J. Lamit, T. G. Whitham, and C. A. Gehring. 2014. Plant genetic identity of foundation tree species and their hybrids affects a litter-dwelling generalist predator. *Oecologia* 176:799–810.
- Woodin, S. A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. *Ecological Monographs* 44:171–187.
- Wymore, A. S., Z. G. Compson, C. M. Liu, L. B. Price, T. G. Whitham, P. Keim, and J. C. Marks. 2013. Contrasting rRNA gene abundance patterns for aquatic fungi and bacteria in response to leaf-litter chemistry. *Freshwater Science* 32:663–672.
- Zytynska, S. E., M. F. Fay, D. Penney, and R. F. Preziosi. 2011. Genetic variation in a tropical tree species influences the associated epiphytic plant and invertebrate communities in a complex forest ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:1329–1336.
- Zytynska, S. E., M. S. Khudr, E. Harris, and R. F. Preziosi. 2012. Genetic effects of tank-forming bromeliads on the associated invertebrate community in a tropical forest ecosystem. *Oecologia* 170:467–475.